

A simplified model to construct food web based on comparative advantage analysis using MERA

Jade, Mar 19

In the last write-up I introduced how to analyze the comparative advantage between competition and predation for a two-species scenario. In the following I will show that this method can be extended to infer the trophic relationship among multiple species, given the sequence they are added into the community. Under this framework, the structure for the food web and the body size distribution among trophic levels emerge.

1 Simplification assumptions

When there are multiple species within a trophic level, unlike the over-simplified scenario in the last write-up, it is likely for multiple (> 1) predator species to compete for multiple prey species. This corresponds to the multi-resource (the resource being the prey species here) scenario of MERA. Although I have taken a first attempt to construct and solve the two-resource MERA equations, the analytical solution is not yet available and the numerical method is still limited (mainly due to the high dimension

and factorial part). Moreover, there is an unresolved problem in the assumption for the two-resource scenario that it cannot be extended to model scenarios with > 2 resources (mostly about the difficulty to account for all possible combinations between the resources which I hope to discuss). To get around this problem, for this extension I introduce one additional assumption (that could be relaxed once the multi-resource MERA is solved):

Species competing for multiple resources (or preys) is equivalent to competing for one resource of the same total energy content.

To elaborate on this, since for now I am only interested in the general structure of the food web (e.g. the number of trophic levels, the species distribution among trophic levels, the body size relationship between species in trophic interactions), I will ignore the explicit patterns of how each prey species is allocated to each predator species, but instead take all species at one trophic level as a lumped “food resource” to the higher trophic level.

For a simple model to start with, I have also assumed that

A predator species is only allowed to prey on species from the next highest trophic level but not any other levels.

Given this and the amount of the fundamental resource R , the resource that can be effectively transformed into steady state biomass (not including those consumed by their predators) of the i_{th} trophic level (from bottom) is

$$\begin{aligned}
R_i &= \frac{R}{2} \times \left(\frac{\tau}{2}\right)^{i-1} && (i \text{ is not the highest trophic level}) \\
&= R \times \left(\frac{\tau}{2}\right)^{i-1} && (i \text{ is the highest trophic level})
\end{aligned} \tag{1}$$

and the constraint at the i_{th} trophic level is just

$$R_i = \sum_j \theta_{i,j} N_{i,j} \tag{2}$$

$\theta_{i,j}$ and $N_{i,j}$ are the resource requirement and abundance for the j_{th} species at the i_{th} trophic level. Notice that R_i and $\theta_{i,j}$ are all in the unit of the fundamental resource. In the manuscript we have proved that as long as D_r is the same for all species, the unit of resource does not affect the steady state abundances. I am not sure whether this is also the case for the multi-resource scenarios but to start with I will just assume **a universal D_r for all species.**

With the above assumptions, we can get the steady state abundance for a species at any trophic level using MERA given the parameters of all the other species at that level, without explicitly specifying how many individuals of each prey species at the lower trophic level it consumes.

2 Construct the food web: add species one by one

Given the above simplification assumptions, we can construct a food web by sequentially adding species into the community. The algorithm can be summarized in four steps: to add a new species into the community,

- 1) when the community is empty, the species forms one (the bottom and the top) trophic level and consumes all resource;
- 2) when the community is not empty, try putting the species into each existing trophic level and calculate its steady state abundance under MERA competition with all the other species of that level subject to the resource constraint (Eq. 2);
- 3) following 2), calculate the steady state abundance of this species if it preys on the current highest trophic level;
- 4) compare all the answers from 2) and 3). If the maximum is from 2), add the species to the trophic level corresponding to the maximum; if the maximum is from 3), add a higher trophic level and put the species into it.

The process is repeated until all species are added.

3 Food web structure: history matters

I simulated 30 species and drew their θ s from a geometric distribution ($p = 0.2$). For all calculations, $R = 10$, $\tau = 0.9$; D_r is assumed to be the same for all species but varied among 0, 0.5 and 0.9 to test its effect.

In the following graphs a), y-axis is the trophic level, each circle indicates one species with the size of it proportional to θ . In graphs b), y-axis is the number of species, x-axis is the trophic level. In both a) and b), a certain

sequence to add species into the community is imposed (from left to right): θ increases through time (the increasing case); θ decreases through time (the decreasing case); sequence is random. Assuming θ is positively related to body size, in the following discussion “body size” and “ θ ” are interchangeable.

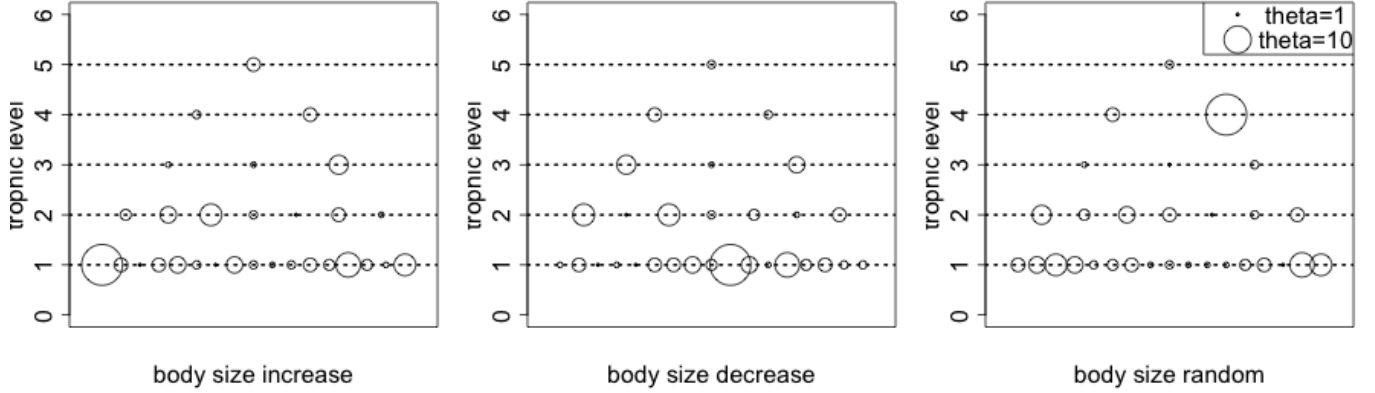


Figure 1. a) Food web structure ($D_r = 0$)

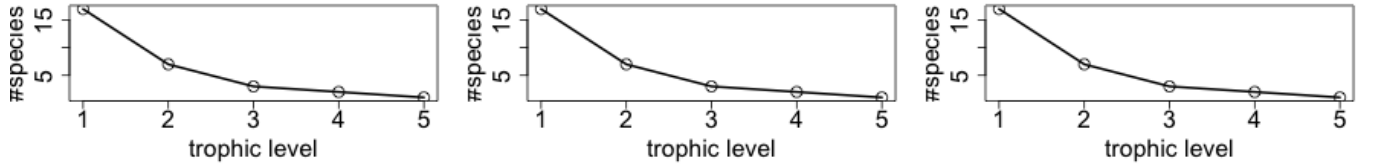


Figure 1. b) Richness variation across trophic level ($D_r = 0$)

From the graphs we could see that when $D_r = 0$ (Fig. 1), the sequence in which species are added does not significantly affect the shape of the food web: the number of trophic levels (=5) and the number of species in each level (shown in Fig. 1b) are the same regardless of the sequence; the body size distribution of the species across trophic levels are also similar.

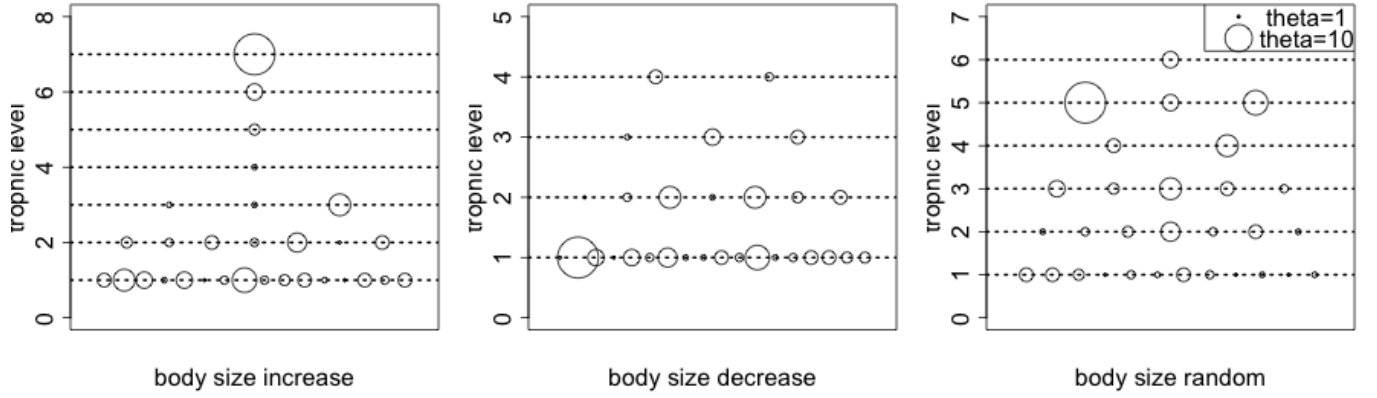


Figure 2. a) Food web structure ($D_r = 0.5$)

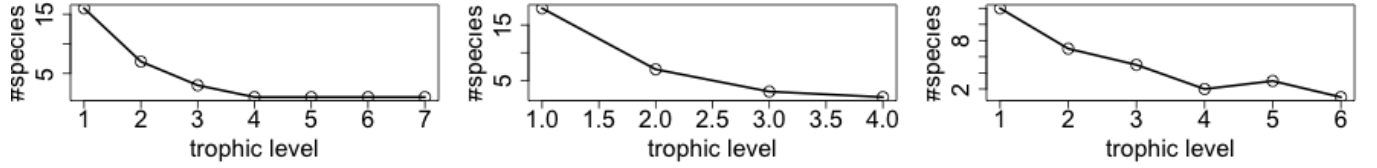


Figure 2. b) Richness variation across trophic level ($D_r = 0.5$)

When $D_r = 0.5$, the patterns for different sequences start to diverge: there are more trophic levels ($=7$) for the increasing case than the decreasing case ($=4$). Partly due to this difference, species are more unevenly distributed for the increasing case: while the number of species are comparable to the decreasing case for trophic level 1 - 3, there is only one species each for trophic level 4 - 7 (the long tail to the right in Fig. 2b). Also, the body sizes of species in higher trophic levels tend to be bigger than those in lower trophic levels for the increasing case while it is the opposite for the decreasing case. For all of the above, the pattern generated by a random sequence is in between the two extremes.

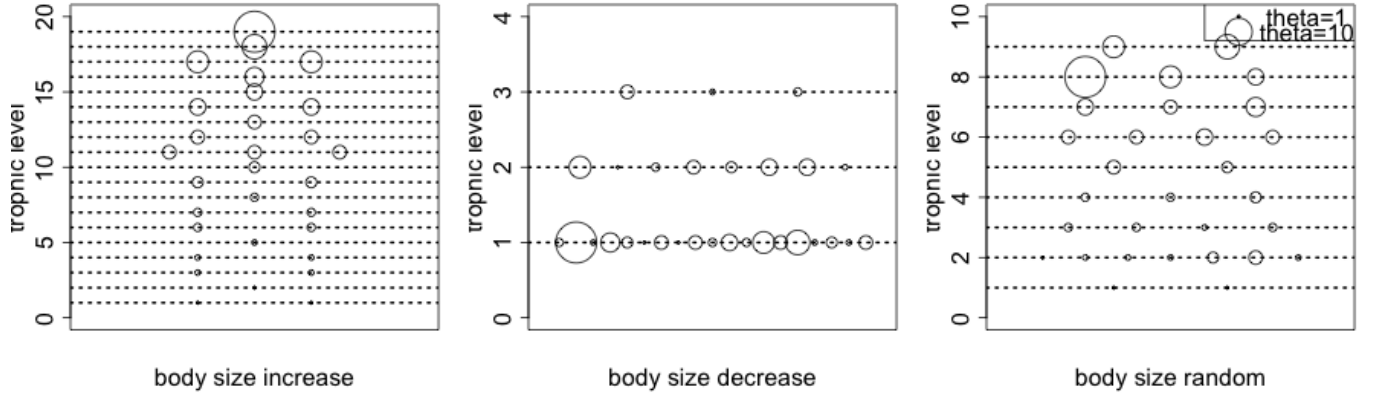


Figure 3. a) Food web structure ($D_r = 0.9$)

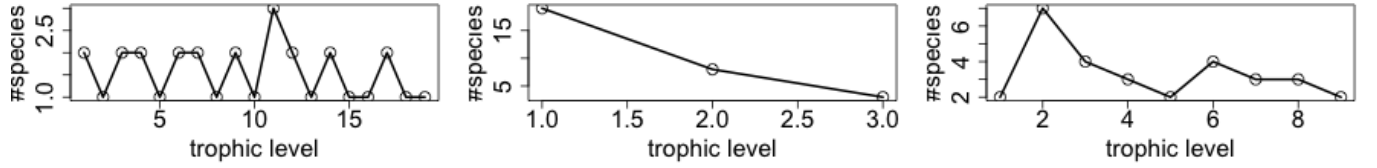


Figure 3. b) Richness variation across trophic level ($D_r = 0.9$)

When $D_r = 0.9$, the differences among cases in Fig. 2 are magnified: there is significantly more trophic levels for the increasing case ($=19$) than the decreasing case ($=3$), meanwhile the contrast in body size distribution is manifested, i.e. body size increases with higher trophic levels for the increasing case and the opposite for the decreasing case. Moreover, the difference in the cross-level variation in the number of species is highlighted (Fig. 3b): while the number of species decreases monotonically with higher trophic level for the decreasing case, it fluctuates drastically for the increasing case and mildly for the random case, a pattern similar to what is observed in nature.

4 Summary

In the above I have shown a preliminary procedure to construct food web from comparative advantage analysis based on MERA. Some general attributes of the resulting food web can be obtained: number of trophic levels, richness distribution and body size distribution among trophic levels. The result has revealed the importance of historical contingency, i.e. the sequence in which species are added, especially when the relative individual distinguishability D_r is big (close to 1).

The procedure has assumed species to be fixed to its position after it enters the community, which is likely the main reason why historical contingency matters that much. The alternative, i.e. species are free to change its position after it enters the community (especially when a new species enters that changes the comparative advantage between trophic levels for an old species), requires more complex algorithm that I am not yet able to realize. It will be my next focus in exploring this direction and thoughts on this are definitely appreciated.

I have used a simplification assumption that lumps each non-top trophic level into a unified food source for its predators. In the future this assumption can also be relaxed and the more detailed energy flow pattern among species between trophic levels be clarified when the multi-resource scenario of MERA is solved.